

# Use of Conifer Snags as Roosts by Female Bats in Western Oregon

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**ABSTRACT** Forest management activities influence habitat suitability for bats, and knowledge of the roosting ecology of bats is fundamental to developing strategies for conserving bats in managed forests. Information on use of roosts by multiple species of bats in a given area may provide insight into interspecific ecological patterns and could improve management prescriptions to provide habitat for bats through time across diverse ownerships and over multiple spatial scales. We investigated use of conifer snags as roosts by females of 3 species of forest-dwelling bats in Douglas-fir (*Pseudotsuga menziesii*) forests in the western Oregon Cascade Range. We radiotagged 29 female big brown bats (*Eptesicus fuscus*), 55 long-legged myotis (*Myotis volans*), and 27 long-eared myotis (*Myotis evotis*) and located 42, 105, and 24 snag roosts for the 3 species, respectively. All 3 species most frequently used Douglas-fir snags and in similar proportions to their availability. Big brown bats and long-legged myotis rarely roosted in stands <40 years old but age of stands used by female long-eared myotis did not differ from those randomly available. Odds of a snag being used as a roost by big brown bats increased with diameter at breast height and decreased with distance from the capture site. Diameter of snags used for roosting and the number of small (10–50 cm dbh) snags within the 20-m radius plot were variables in the best model for roost use by long-legged myotis. The best model for long-eared myotis included distance to the capture site. Odds of a snag being used by female long-eared myotis decreased with increasing distance from the capture site. There was considerable overlap in structural characteristics and the physical context of roost snags among the 3 species, but the types of roosts used among landscapes with differing densities of snags differed among the 3 species. Although big brown bats and long-legged myotis used only snags and live trees as roosts, long-eared myotis used a diversity of structures and the frequency of use of these structures differed with density of snags in the landscape. Relative to other roost types, frequency of use of snags by long-eared myotis was nearly twice as high in landscapes with high densities of snags as in those with low densities. We found that some species of bats alter selection of roosts depending on landscape context and availability of different types of roosts. Our findings demonstrate that forest managers must consider the needs of multiple bat species and the distribution of roosts in the landscape, especially where densities of snags are low and at low elevations in intensively managed landscapes. (JOURNAL OF WILDLIFE MANAGEMENT 73(2):214–225; 2009)

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Knowledge of the roosting ecology of forest-dwelling bats is fundamental for understanding the impact of management activities and for developing strategies to conserve bats (Barclay and Kurta 2007, Hayes and Loeb 2007). Roost selection by bats is likely influenced by factors including diversity and abundance of roosts, distribution and abundance of prey, distribution of roosts in relation to foraging areas, and bioenergetics (Kunz and Lumsden 2003, Broders and Forbes 2004, Barclay and Kurta 2007). Availability of suitable roosts is postulated to be a determinant of abundance and distribution of temperate zone bats (Humphrey 1975, Kunz 1982, Hayes 2003, Hayes and Loeb 2007). In some situations, populations may be limited by availability of roosts suitable for use during reproduction (Lewis 1995). High use of mature and old-growth forests (Perkins and Cross 1988, Thomas 1988, Crampton and Barclay 1998, Humes et al. 1999) may be, in part, a consequence of availability of large, older trees for roosting in these stands (Kunz 1982, Crampton and Barclay 1998, Hayes 2003, Barclay and Kurta 2007). Although distribution and availability of roosts influences behavior and habitat

use by other species (e.g., Brigham 1991), use of roost structures among landscapes with varying availability of snags is largely unknown.

Studies of resource partitioning in bat communities have largely focused on food resources and use of habitats for foraging (e.g., Aldridge and Rautenbach 1987, Saunders and Barclay 1992, Warren et al. 2000, Lee and McCracken 2004). Little data exist on differences in use of roosts by sympatric bat species and it is unknown whether sympatric species partition available roosts (Kunz and Lumsden 2003). Previous research suggested that roost characteristics should be similar among species (e.g., Vonhof and Barclay 1996), and at a coarse level this is generally true (Hayes 2003). Some studies suggest little or no difference in roost characteristics of sympatric bats (e.g., Crampton and Barclay 1998, Psyllakis and Brigham 2006) and others have documented inter- and intraspecific selection of different roost characteristics at different scales (Lumsden et al. 2002a, b; Chung-MacCoubrey 2003; Broders and Forbes 2004). Whether species-specific differences in the type of roost used or specific characteristics of roosts are sufficient to reduce competition for roosts among species remains unknown (Barclay and Kurta 2007).

Most roost selection studies have focused on one species. Investigating multiple species in the same landscapes

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should facilitate improved management prescriptions through time across diverse ownerships and over multiple spatial scales (Chung-MacCoubrey 2003). Moreover, information on roost use by multiple bat species in a given area will provide insight into interspecific patterns relevant to the community ecology of bats. We studied use of conifer snags as day roosts by females of 3 sympatric forest-dwelling bats, the big brown bat (*Eptesicus fuscus*), the long-legged myotis (*Myotis volans*), and the long-eared myotis (*Myotis evotis*), in managed Douglas-fir (*Pseudotsuga menziesii*) forests in the western Oregon Cascade Range. Our objectives were to determine 1) characteristics of snags selected by each species, 2) the role of characteristics (e.g., diam, ht) and context (e.g., elevation, aspect, proximity to resources) of roosts in differentiating snags used as roosts by the 3 species of bats, and 3) if types of roosts (e.g., snags, trees, stumps, downed logs) used varied with landscape context.

## STUDY AREA

We conducted this study in the Western Cascades physiographic province along the west slope of the Cascade Mountain Range in Oregon, USA. The study area stretched from the Calapooya River and east of Springfield, Oregon, south to the North Umpqua River east of Roseburg, Oregon (43°25'N and 44°20' N and 122°25'W and 123°25' W) and is characterized by a maritime climate with wet, mild winters and cool, dry summers (Franklin and Dyrness 1988). Elevation ranged from 150 m to >1,500 m.

The study area was dominated by natural and planted stands of Douglas-fir but other conifers included western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Red alder (*Alnus rubra*) was abundant in riparian areas and disturbed sites. Bigleaf maple (*Acer macrophyllum*) was also common throughout the study area in upland and riparian areas. Understory vegetation was typically dominated by salmonberry (*Rubus spectabilis*), thimbleberry (*Rubus parviflorus*), salal (*Gaultheria shallon*), huckleberry (*Vaccinium* spp.), red elderberry (*Sambucus racemosa*), vine maple (*Acer circinatum*), and swordfern (*Polystichum munitum*). The study area was a mix of public and private lands with diverse management histories, objectives, and habitats. Public lands encompassed a mix of late-successional forest reserves within a matrix of younger managed stands. These forests were managed for multiple use objectives that included late-successional habitat, recreation, fish and wildlife habitat, and timber production (U.S. Forest Service and Bureau of Land Management 1994). Private commercial forests were managed primarily for wood production. Intensive high-yield timber management was practiced since the mid-1960s and usually included planting nursery-grown seedlings, fertilization, control of competing deciduous vegetation, precommercial and commercial thinning, and clear-cutting on 45–60-year rotations. The young conifer forest was interspersed with riparian reserves, recent clear-cuts, and small gaps associated with streams, topography, and roads.

## METHODS

We defined potential capture sites as ponds with dimensions between 5 × 5 m and 20 × 20 m, allowing us to use standard mist nets, or bridges with I-beam construction over large, fish-bearing streams located ≥1.6 km from any house or barn (Lorensen et al. 1994). Once we identified all possible capture sites, we estimated the amount of forest >80 years old in a 2.4-km-radius circle (1,828 ha) surrounding the potential site using a Geographic Information System (GIS; ArcGIS version 6.0) and forest inventory data from Weyerhaeuser's Calapooya Tree Farm, which also included forest age-class data from the United States Bureau of Land Management. We categorized each 2.4-km-radius circle as having a low (0–100 ha), medium (101–250 ha), or high (>250 ha) area of >80-year-old forest and randomly selected 12 ponds in each of the 3 categories ( $n = 36$ ) and 12 bridges (4 in each category) for capture efforts. Once we selected a given site, we eliminated all other potential sites within 1.6 km. Because we only captured big brown bats, long-legged myotis, or long-eared myotis at 8 of the bridge sites, we used 44 landscapes (36 pond sites and 8 bridges) in our study.

We captured bats at ponds using mist nets (Avinet, Dryden, NY) and at bridges using handheld mist nets (Waldien and Hayes 1999) or hoop nets from late May through early September 1999–2001. We recorded species, sex, age, and reproductive status for all bats captured following Anthony (1988) and Racey (1974, 1988). We determined age based on degree of ossification in the joints of the phalanges of the third metacarpal (Racey 1974) and determined pregnancy by palpating the abdomen of females. We considered females that secreted milk lactating, whereas those with obvious suckle marks around the nipple who did not secrete milk were postlactating.

We attached radiotransmitters (0.45–0.54 g Model LB 2; Holohil Systems Ltd., Carp, ON, Canada) to adult female big brown bats, long-legged myotis, and long-eared myotis with body mass >6.0 g as evenly among species and across sampled landscapes and the sampling period as possible. We clipped a small amount of fur from between the scapula and attached transmitters with Skinbond surgical adhesive (Smith & Nephew, Inc., Largo, FL). We held radiotagged bats for 20 minutes to allow the glue to set and then released them at the capture site. The ratio of transmitter to body mass ranged from 1.9–3.1% for big brown bats (0.52–0.54-g transmitters, 17.0–25.7-g bats), 4.7–7.1% for long-legged myotis (0.47–0.52-g transmitters, 6.6–10.0-g bats), and 5.5–7.8% for long-eared myotis (0.45–0.48-g transmitters, 6.0–8.5-g bats). Of the 59 tagged long-legged myotis, 4 had a transmitter-to-body mass ratio of <5% (Aldridge and Brigham 1988), 33 had transmitters that were 5.1–6.0% of total body weight, and 22 were 6.1–7.1% of total body weight. Of the 29 tagged long-eared myotis, 8 had a transmitter-to-body mass ratio of 5.5–6.0%, 13 had transmitters that were 6.1–7.0% of total body weight, and 9 were 7.1–7.8% of total body weight. We conducted captures and all animal handling procedures in accordance with permits

and processes issued by the Oregon Department of Fish and Wildlife (permit no. 116-99, 003-00, and 021-01) and the Institutional Animal Care and Use Committee at Oregon State University (AUF no. 2241).

We used Wildlife Materials TRX-1000S and 2000S receivers (Wildlife Materials, Inc., Carbondale, IL) and handheld 3- and 5-element yagi antennas to track bats to roosts. We attempted to track each radiotagged individual each day until the transmitter failed or was shed. If a tagged bat did not switch roosts on consecutive days, we verified that it was still alive or had not shed its transmitter by monitoring the radio signal nocturnally or by visually observing bats emerging from day roosts at dusk. If the bat did not emerge for 3 days, we assumed the transmitter was shed or the bat had died. We did not include in our analysis structures for which there was no evidence that the bat had left the roost at least once to prevent misclassification of structures where a transmitter had been shed by bats in night roosts or while flying over the structure (Waldien et al. 2000). We geo-referenced with a Trimble Pathfinder Pro XL Global Positioning System ( $\pm 1$  m accuracy) each structure used as a day roost.

We tagged 137 females (50 big brown bats, 59 long-legged myotis, and 29 long-eared myotis). We never found 9 tagged big brown bats, 4 long-legged myotis, and 1 long-eared myotis individual and we assumed that they left the study area or were tagged with defective radios. Additionally, we excluded from analysis data for 12 big brown bats that only used houses as day roosts and long-eared myotis that traveled outside the landscape area. Thus, we used data for roosts used by 29 big brown bats, 55 long-legged myotis, and 27 long-eared myotis in our analyses.

Greater than 95% of day roosts were within 4.8 km of capture sites and 99% of roosts used by long-eared myotis were within 2.4 km of the capture site. Thus, we used 2.4-km-radius circles to define landscapes for long-eared myotis and 4.8-km-radius circles (7,326 ha) for big brown and long-legged myotis for locating random points, measuring habitat variables, and conducting habitat analyses. Selection of structures used for roosting by bats is most commonly investigated by comparing attributes of roosts with those of randomly selected structures in the immediate vicinity or in the same stand (Miller et al. 2003, Barclay and Kurta 2007). In contrast, we sampled randomly selected snags and trees at the landscape scale based on the assumption that any bat captured and radiomarked at a site had equal chance of flying to any point within the landscape to select a snag or tree for roosting.

To randomly locate snags and trees for comparisons, we used ArcGIS 8 to generate 250 random points in each landscape. We then randomly selected points for sampling from all possible points available (44 landscapes  $\times$  250 points in each landscape yielded 11,000 landscape-point combinations). At each selected sample point, we established a 100-m-long transect along the first randomly selected direction that allowed for the 100-m transect to be established within the stand. We selected the first snag or

tree encountered within 20 m of either side of the transect line. If we did not encounter a snag or tree along the transect, we established up to 3 additional transects at the point. If we found no tree or snag on any transects, we discarded the point and sampled the next randomly selected point. Although we identified no randomly selected structure as used by radiotagged bats during our study, it is possible that some were used.

We measured or estimated characteristics of trees and surrounding plots and landscapes that have been suggested to be important factors influencing use of snag and tree roosts by forest-dwelling bats (Lacki and Baker 2003, Barclay and Kurta 2007) for each roost and randomly selected structure we sampled. We categorized each snag as conifer or hardwood and, when possible, identified it to species. We measured diameter at breast height (cm) and height (m) of each snag. We visually estimated percentage of bark remaining for each snag and assigned it to one of 6 decay classes based on Brown (1985), which we later collapsed into 3 categories following Waldien et al. (2000). We recorded total number of snags  $\geq 10$  cm diameter at breast height and  $> 3$  m tall (Waldien et al. 2000) and measured height of the dominant canopy with a laser range finder in the 20-m-radius (0.15-ha) plot centered on each roost or randomly selected structure.

We used ArcGIS 8 and a United States Geological Survey 10-m digital elevation model to determine elevation, percentage of slope, and aspect of each roost and randomly selected structure. We used the line statistic analysis tool in ArcGIS Spatial Analyst to calculate distance from a roost or random structure to the capture site and to the nearest pond with open water. We created a forest cover layer using 1-m digital orthophotography (circa 2000) from the State of Oregon (Oregon Geospatial Enterprise Office 2007) and overlaid it with coordinates of all roosts and random points. We added a stream layer based on a database from the Oregon Department of Forestry that included all medium (average annual flow  $> 0.04$  m<sup>3</sup> and  $< 0.2$  m<sup>3</sup>/sec) and large (average annual flow  $\geq 0.2$  m<sup>3</sup>/sec) permanent streams (Lorenson et al. 1994, Oregon Department of Forestry 1997). We used the linear measurement tool in ArcView to determine distance from each roost and random point to closest medium or large perennial stream and to the nearest edge of a gap in the canopy of a forested stand (an opening in the forest  $\geq 20$  m wide) or the edge of an adjacent stand. We used ArcView to center a scale-equivalent (i.e., 1:12,000) 20-m-radius plot on each roost and random point and we visually estimated canopy closure to the nearest 5% class for each plot.

To determine age of the stand for each roost and randomly selected structure and to estimate density of snags in landscapes, we created a database using ArcGIS by merging forest stand inventory data provided by timber companies and federal agencies. The generated layer included 8 classes based on stand age and land ownership: 0-10 years, 11-20 years, 81-200 years, and  $> 200$  years for any ownership and 21-40 years and 41-80 years for plots in private ownership



or federal ownership. We assumed stand age was correctly classified by each owner. Spatial inconsistency associated with edge matching in our merged dataset was <1% of the total area encompassed by our study area. Our first-level stratification yielded a data layer that constituted between 40% and 100% of the available area for each landscape. Proportions of each landscape not accounted for by forest inventory data were generally private, nonindustrial lands (PNI) and we classified them as such. To quantify proportion of PNI lands and create 100% area coverage for each landscape, we digitized a stand polygon layer using 1-m digital orthophotography (circa 2000) from the State of Oregon (Oregon Geospatial Enterprise Office 2007). We were unable to reliably assign the same stand classes derived from forest inventory data to our digitized PNI stand polygons. Thus, we collapsed the 21–40-year and 41–80-year classes to one class and created 5 broad classes and assigned each PNI polygon to one of the following: non-forest, 0–10-year-old, 11–20-year-old, 21–80-year-old, and >80-year-old stands. We used forest inventory polygons of known age that were adjacent to a PNI forest polygon in question and visually compared them to identify the stand class as accurately as possible.

We quantified snag density (snags/ha) for each stand class using the methods of Bate et al. (1999; see Arnett 2007 for details). We estimated number of snags in a landscape by summing the estimated number of snags in each stand class in the landscape ([mean no. of snags >25.4 cm dbh, >3 m tall, in decay classes 2–6/ha]  $\times$  [no. of ha of that stand type occurring on the landscape]). We used the mean of the densities of snags estimated for stand classes 21–40 years and 41–80 years from private lands as an estimate of mean density of snags for PNI stand class 21–80 years. Similarly, we used mean snag density/ha for 81–200-year-old and >200-year-old stands to calculate an estimate for PNI stands >80 years old. Based on these calculations, we classified each landscape as having a low (<20,000 snags in the landscape, <2.7 snags/ha;  $n = 14$ ), medium (20,000–40,000, 2.7–5.5/ha,  $n = 12$ ), or high (>40,000, >5.5/ha,  $n = 10$ ) density of snags.

### Data Analysis

We pooled data across years to determine which characteristics differentiated between roost and random snags for each species. We excluded roosts located >2.4 km from the capture site for long-eared myotis ( $n = 1$ , of 25 roosts identified for this species) and >4.8 km from the capture site for long-legged myotis ( $n = 12$ ) from the analyses; all roosts used by big brown bats were within 4.8 km of the capture site. We removed hardwood snags ( $n = 5$ ; 4%) used by long-legged myotis from our analyses of characteristics of snags and trees selected because of small sample size. We included 42 conifer snags for big brown bats, 105 for long-legged myotis, and 24 for long-eared myotis in our analysis and only used random conifer snags from landscapes where we found  $\geq 1$  roost for that species in our models. Also, we only used those random snags that were located within 2.4-km-radius landscapes used by long-eared myotis and within

4.8-km-radius landscapes used by big brown bats or long-legged myotis. We counted snags used by >1 individual of the same species ( $n = 7$  for big brown bats,  $n = 3$  for long-legged myotis) only once for our analysis. On 2 occasions, 2 snags were used by 2 species; we counted these snags once in the model for each species.

We used Fisher's exact test (PROC FREQ, SAS Institute, Cary, NC) to compare frequencies of stand age classes for snags used as roosts to those for random snags. We combined stands <40 years old on private and federal ownership into one category. We also used Fisher's exact test to compare frequencies of roost and random snags by species of tree and to compare frequencies of types of structures (i.e., trees, snags, stumps, logs) used as roosts by female bats in landscapes estimated to have low, medium, and high density of snags. For the latter analysis, we combined snags and trees into one category and stumps and down logs into another category.

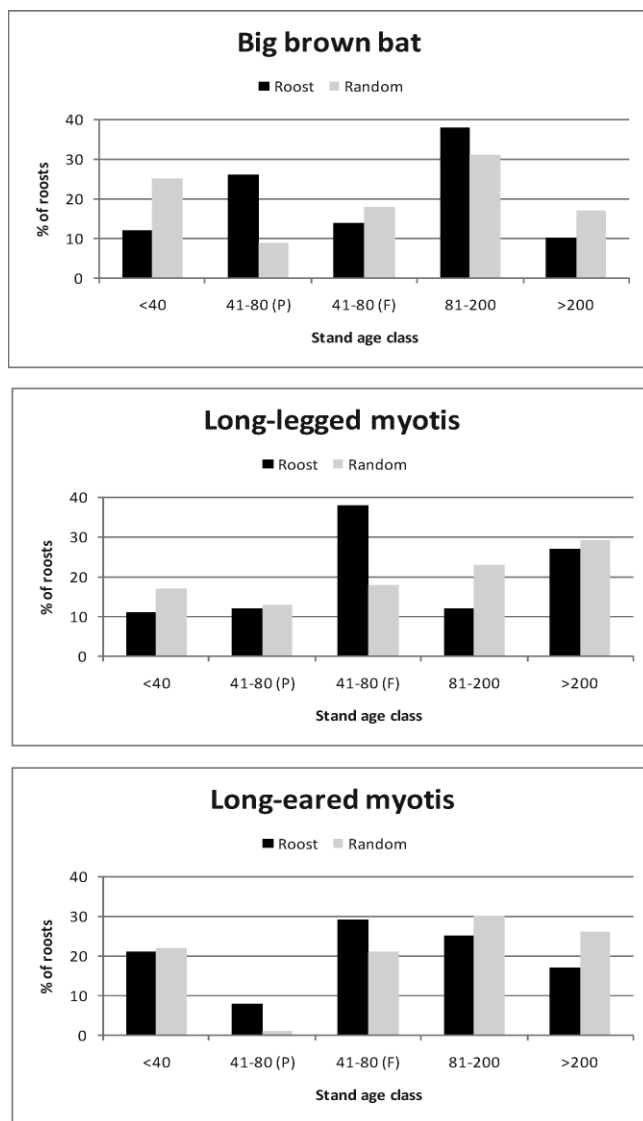
For our roost selection models, we created a new variable for aspect by using a cosine transformation of the azimuth for each roost and random point ( $\cos\text{asp} = \cos[\text{azimuth}/360] \times 2 \times \pi$ ). We also created a variable reflecting the position of a snag relative to its solar exposure and ease of access by bats (solar; Appendix). We coded a roost or random snag as 1 if it had a roost:dominant canopy ratio >1, its distance to an edge or gap was <10 m, or its canopy closure was <25%; we coded the structure as 0 if none of these criteria were met.

To determine which characteristics best differentiated between used and randomly selected snags for each species, we developed 27 candidate models that focused on how diameter of snags changed in relation to changes in stand and landscape variables (Appendix). We used logistic regression (PROC GENMOD, SAS Institute) to estimate model parameters and compared models using the small sample variant of Akaike's Information Criterion ( $AIC_c$ ) based on  $AIC_c$  differences ( $\Delta$ ) and Akaike weights ( $w_i$ ; Burnham and Anderson 2002). We considered models with  $\Delta < 2$  to be competitive (Burnham and Anderson 2002). We calculated Nagelkerke's  $R$ -square value for generalized linear models (Nagelkerke 1991) as a measure of the coefficient of determination for each model. We calculated odds ratios by exponentiation of the parameter estimates (Hosmer and Lemeshow 1989).

To determine whether structural characteristics or the physical context of roosts best differentiated snags used as roosts by female bats, we used classification and regression tree (CART) analysis to generate a classification tree to separate roosts used by the 3 species (Venables and Ripley 1994). Classification trees generated by CART produce a set of logical if–then conditions for predicting or classifying cases (i.e., snag or tree roosts). Decisions are made at  $\geq 1$  branch nodes and based on values of specific variables that sort each case into a designated group (Venables and Ripley 1994).

## RESULTS

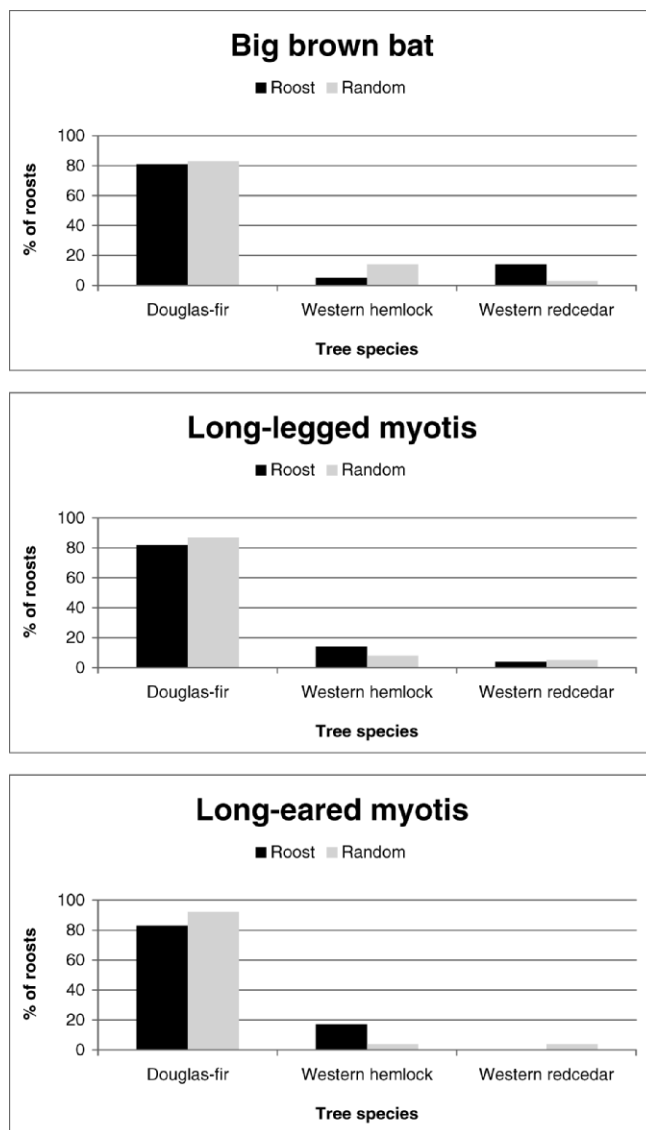
We tracked big brown bats from 1 day to 18 days ( $\bar{x} = 10.2$ ,  $SE = 0.9$ ), and bats used 1–8 unique roosts ( $\bar{x} = 2.8$ ,  $SE =$



**Figure 1.** Number (%) of roost and random snags among forest stand age classes (P = private land, F = federal land) for female big brown bats, long-legged myotis, and long-eared myotis in the western Oregon Cascade Range, 1999–2001.

0.3) and switched roosts 0–10 times ( $\bar{x} = 2.9$ , SE = 0.5). Long-legged myotis used 1–8 unique roosts ( $\bar{x} = 2.8$ , SE = 0.2) during 1–18 days of radiotracking ( $\bar{x} = 8.4$ , SE = 0.6), and switched roosts 0–8 times ( $\bar{x} = 2.5$ , SE = 0.3). We tracked long-eared myotis from 1 day to 15 days ( $\bar{x} = 7.5$ , SE = 0.6), and bats used 1–7 unique roosts ( $\bar{x} = 3.4$ , SE = 0.3) and switched roosts 0–7 times ( $\bar{x} = 2.7$ , SE = 0.4).

Frequency of snags used as day roosts by big brown bats differed among stand age classes compared to those randomly available ( $\chi^2 = 11.10$ ,  $P = 0.033$ ; Fig. 1). Big brown bats most frequently roosted in snags in 81–200-year-old stands, with 12% of snags used as roosts and 25% of randomly selected snags located in stands <40 years old. Twenty-six percent of big brown bat snag roosts were found in 41–80-year-old stands on private land compared to 9% of random snags (Fig. 1). Big brown bats roosted in snags in >200-year-old stands and 41–80-year-old stands on federal



**Figure 2.** Number (%) of roost and random snags among tree species for female big brown bats, long-legged myotis, and long-eared myotis in the western Oregon Cascade Range, 1999–2001.

land in nearly equal frequency to random snags (Fig. 1). Patterns of use for long-legged myotis differed from distribution of randomly available snags ( $\chi^2 = 10.83$ ,  $P = 0.029$ ; Fig. 1). Long-legged myotis infrequently roosted in snags in stands <40 years old, and 7 of 12 snag roosts found in these stands were located within riparian management buffers near small- and medium-sized perennial streams. Long-legged myotis roosted in snags in 41–80-year-old stands on federal land (38%) more frequently than available (18%). Frequency of snags used as roosts in 81–200-year-old stands (12%) was less than those of randomly selected snags used as roosts by this species (23%; Fig. 1). Frequency of snags used as day roosts by long-eared myotis among stand age classes did not differ from randomly available snags ( $\chi^2 = 2.79$ ,  $P = 0.732$ ; Fig. 1).

Frequency of use of different species of snags used by big brown bats differed from that of randomly selected snags ( $\chi^2 = 8.72$ ,  $P = 0.015$ ; Fig. 2). Big brown bats roosted most

**Table 1.** Variables, number of estimable parameters in the model ( $K$ ), difference in Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ) score between the  $i$ th and top-ranked model with the lowest  $AIC_c$  value ( $\Delta_i$ ),  $AIC_c$  weights ( $w_i$ ), sum of  $AIC_c$  weights ( $\sum w_i$ ), and Nagelkerke's  $R$ -square value ( $R^2_N$ ) for competing models and the null model explaining differences between roost and random snags for females of three species of bats in the western Oregon Cascades, 1999–2001.

Model	$K$	$\Delta_i$	$w_i$	$\sum w_i$	$R^2_N$
Big brown bat					
Dbh	3	0.00	0.43	0.43	0.44
Distance to capture site					
Dbh	4	0.80	0.29	0.72	0.45
No. of large snags					
Dbh $\times$ no. of large snags interaction					
Dbh	4	1.47	0.20	0.92	0.45
Distance to capture site					
Dbh $\times$ distance to capture site interaction					
Null	1	49.80	<0.01		0.00
Long-legged myotis					
Dbh	3	0.00	0.59	0.59	0.35
No. of small snags					
Dbh	4	1.16	0.33	0.92	0.35
No. of small snags					
Dbh $\times$ no. of small snags interaction					
Null	1	64.10	<0.01		0.00
Long-eared myotis					
Distance to capture site	2	0.00	0.60	0.60	0.43
Dbh	3	1.56	0.27	0.87	0.46
Distance to capture site					
Null	1	16.20	<0.01		0.00

frequently in Douglas-fir snags ( $n = 34$ , 81%) at a frequency similar to randomly selected snags ( $n = 86$ , 83%). Only 2 western hemlock snags (5%) were used by big brown bats compared to 14% ( $n = 15$ ) of randomly selected snags, whereas 14% ( $n = 6$ ) of snags used as roosts were western redcedar compared to 3% ( $n = 3$ ) of randomly selected snags (Fig. 2). Long-eared myotis and long-legged myotis also roosted most frequently in Douglas-fir snags but at a frequency that did not differ from that of randomly available snags ( $\chi^2 = 2.80$ ,  $P = 0.35$  for long-eared myotis,  $\chi^2 = 2.74$ ,  $P = 0.27$  for long-legged myotis; Fig. 2). We found no female long-eared myotis roosting in western redcedar snags.

The best model for use of snags by big brown bats included diameter of snags and distance to the capture site (Table 1). Odds of a snag being used as a roost by big brown bats increased 29% (odds ratio [OR] = 1.29; 95% CI = 1.15–1.43) for each 10-cm increase in diameter and decreased 8% (OR = 0.92; 95% CL = 0.88–0.95) for every 100-m increase in distance from the capture site (Table 2). A competing model included diameter, number of large (>50 cm dbh) snags within 20 m, and the interaction between diameter and large snags (Table 1). When there were no large snags within a 20-m-radius plot around a snag, odds of the snag being used as a roost by big brown bats increased by 40% (OR = 1.40; 95% CI = 1.21–1.62) for each 10-cm increase in diameter at breast height (Table 2). When there were 2 large snags within a 20-m-radius plot around a snag, odds of it being a roost used by big brown bats increased 18% (OR = 1.17; 95% CI = 1.06–1.31) for each 10-cm increase in diameter at breast height. However, the relationship diminished as number of large snags increased to >2. A second competing model included

diameter, distance to the capture site, and the interaction between diameter and distance (Table 1). When a snag was 500 m from the capture site, odds of it being a roost increased by 21% (OR = 1.21; 95% CI = 1.01–1.44) for each 10-cm increase in diameter. Effect of diameter was stronger as distance increased, with odds of a snag being used by big brown bats increasing by 38% (OR = 1.38; 95% CI = 1.12–1.72) for each 10-cm increase in diameter when the snag was 4.5 km from the capture site.

Diameter and number of small (10–50 cm dbh) snags within 20-m-radius plots were variables in the best model for use of snags by long-legged myotis (Table 1). A competing model included diameter, number of small snags, and the interaction between diameter and small snags. The 2 top models constituted 92% of the weight of evidence from the candidate model set (Table 2). Based on the top model, odds of a snag being used as a roost by long-legged myotis increased 19% (OR = 1.19; 95% CI = 1.10–1.28) for each 10-cm increase in diameter at breast height and increased 58% (95% CI = 1.35–1.86) for each small snag included within 20 m of the snag (Table 2). From the competing model, when there were no small snags within 20 m of a snag, odds of it being a roost increased by 15% (OR = 1.15; 95% CI = 1.06–1.27) for each 10-cm increase in diameter at breast height. When there were 4 small snags within 20 m of a snag, odds of it being a long-legged myotis roost increased 26% (OR = 1.26; 95% CI = 1.08–1.48) for each 10-cm increase in diameter at breast height. The odds of a snag being used as a roost by increased to 38% (OR = 1.38; 95% CI = 0.99–1.92) for each 10-cm increase in diameter at breast height when there were 8 small snags within 20 m.

The best model for long-eared myotis included distance to the capture site (Table 1). Odds of a snag being used as a

**Table 2.** Parameter estimates, standard errors, odds ratios, and 95% confidence limits for best approximating models and competing models (those <2 Akaike's Information Criterion units from the best model) differentiating between used and random snags for female big brown bats, long-legged myotis, and long-eared myotis in the western Oregon Cascades, 1999–2001.

Variable	Estimate	SE	Odds ratio	95% CL
Big brown bat				
Intercept	−1.132	0.657		
Dbh	0.251	0.055	1.285	1.154–1.431
Distance to capture site	−0.089	0.019	0.915	0.879–0.951
Long-legged myotis				
Intercept	−5.121	0.921		
Dbh	0.338	0.073	1.402	1.214–1.619
No. of large snags	1.533	0.404	4.633	2.099–10.22
Dbh × no. of large snags interaction	−0.009	0.003	0.991	0.986–0.997
Long-eared myotis				
Intercept	−0.314	1.196		
Dbh	0.173	0.108	1.189	0.962–1.470
Distance to capture site	−0.127	0.052	0.881	0.795–0.975
Dbh × distance to capture site interaction	0.003	0.004	1.003	0.999–1.001
Long-legged myotis				
Intercept	−2.487	0.421		
Dbh	0.172	0.038	1.188	1.100–1.280
No. of small snags	0.459	0.083	1.582	1.346–1.862
Long-eared myotis				
Intercept	−2.313	0.453		
Dbh	0.148	0.045	1.160	1.060–1.267
No. of small snags	0.337	0.149	1.400	1.046–1.876
Dbh × no. of small snags interaction	0.002	0.002	1.002	0.998–1.007
Long-eared myotis				
Intercept	2.629	0.801		
Distance to capture site	−0.259	0.077	0.770	0.660–0.901
Long-eared myotis				
Intercept	3.266	1.147		
Dbh	−0.083	0.098	0.920	0.759–1.116

roost by long-eared myotis decreased 23% (OR = 0.77; 95% CL = 0.66–0.90) for every 100-m increase in distance (Table 2). A competing model included diameter at breast height and distance (Table 1). In this model, odds of a snag being used as a roost by long-eared myotis increased 8% (OR = 0.92; 95% CI = 0.76–1.12) for each 10-cm increase in diameter at breast height and decreased 23% (OR = 0.77; 95% CL = 0.66–0.90) for every 100-m increase in distance.

All 3 species of bats used Douglas-fir snags as roosts with nearly equal frequency (Fig. 2). Big brown bats used western hemlock snags less frequently than did long-eared or long-legged myotis and western redcedar more frequently than the other 2 species. Long-eared myotis did not use western redcedar snags as roosts. We correctly classified with the CART analysis 85% of snags used as roosts by female big brown bats, long-eared myotis, and long-legged myotis. Distance to capture site was the variable that best distinguished use of snags as roosts by long-eared myotis relative to the other species (Fig. 3). Eighty-eight percent (21/24) of snags used by long-eared myotis, 17% (7/42) of snags used by big brown bats, and 38% (40/105) of snags used by long-legged myotis were <915 m from the capture site. Other structural and context variables did not clearly identify roosts used by either big brown bats or long-legged myotis. These 2 species exhibited considerable overlap in use of snags.

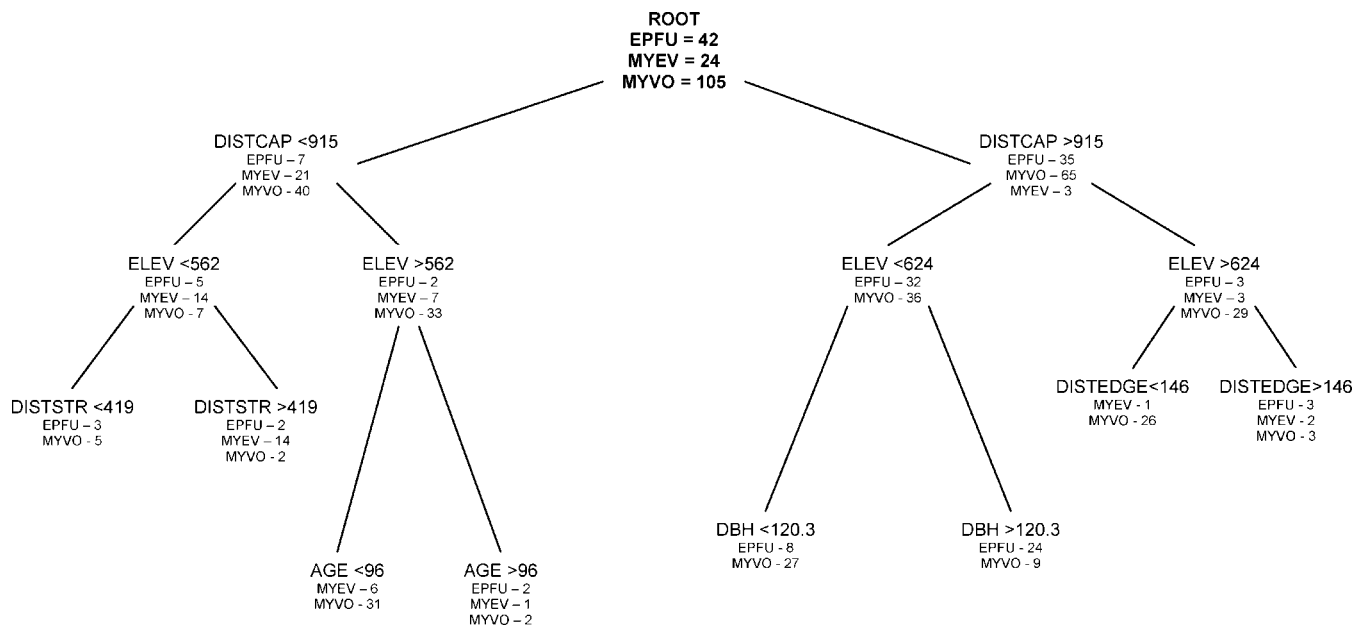
With the exception of a few buildings used as roosts by big brown bats, this species and long-legged myotis only used snags and live trees as roosts (Fig. 4). However, long-eared myotis used a diversity of roost structures. Frequency of use of different roost types differed with density of snags in the

landscape ( $\chi^2 = 17.3$ ,  $P < 0.001$ ). Frequency of use of snags and trees by long-eared myotis increased with increasing density of snags and was nearly twice as high in landscapes with a high density of snags. Conversely, frequent use of stumps and logs was higher in landscapes with low and medium densities of snags (Fig. 4).

## DISCUSSION

Odds of snags being used as roosts by females of all 3 bat species increased with increasing diameter, a common finding in roost selection studies (Hayes 2003, Lacki and Baker 2003, Kalcounis-Rüppell et al. 2005, Barclay and Kurta 2007). Large-diameter trees tend to be in more open areas or extend above the canopy, presumably enhancing access and increasing exposure to solar radiation, which would contribute to cavity warming (Hayes 2003, Kunz and Lumsden 2003, Barclay and Kurta 2007). Also, the thermal inertia and insulating properties of wood and bark increase with diameter, making for greater thermal stability (Sedgeley 2001, Hayes 2003, Kunz and Lumsden 2003, Barclay and Kurta 2007). Increased warmth in a roost should reduce energetic demands on females and facilitates development and growth of young (Racey 1973, Racey and Swift 1981, Kunz 1982). Bats also may use large snags and trees simply because they are of sufficient age and size to have developed numerous cavities or more exfoliating bark area that support more occupants (Sedgeley 2003, Barclay and Kurta 2007). Indeed, big brown bats and long-legged myotis form large colonies in roost trees, and size of colonies is positively related to size of cavities, roost trees, and amount of bark remaining (Brigham 1991, Willis and Brigham 2004, Baker





**Figure 3.** Classification and regression tree partition of characteristics of snags used as day roosts by female big brown bats (EPFU), long-eared myotis (MYEV), and long-legged myotis (MYVO) in the western Oregon Cascade Range, 1999–2001. Number of roosts for each species at each partition appears to the right of the species acronym. Characteristics of snags included distance to capture site (DISTCAP), elevation (ELEV), distance to stream (DISTSTR), distance to stand edge (DISTEDGE), stand age, and diameter at breast height (DBH). All distances are in meters.

and Lacki 2006, Willis et al. 2006). Conversely, long-eared myotis typically roost solitarily or in small groups (Waldien et al. 2000), which may explain their use of smaller-diameter snags and trees.

We found that selection of roost snags can vary with the spatial context of the roost and that characteristics of selected snags are sometimes influenced by landscape context. Barclay and Kurta (2007) suggested that characteristics of roosts themselves are more important than proximity to resources. Our data suggest that both structural characteristics and physical context can be important determinants of roost selection. Particularly intriguing is evidence that big brown bats exhibit the strongest response to increasing diameter as potential roost sites increase with distance from the capture site, which suggests that these bats may seek larger-diameter trees and snags that are farther from water at capture sites. Similarly, diameter of snags used by big brown bats and long-legged myotis was influenced by number of snags present nearby, with big brown bats apparently using the largest-diameter trees when few or no snags are adjacent. The underlying mechanisms responsible for apparent interactions between characteristics of snags selected and the context within which the snag occurs are not clear, but selection of roosts likely results from a complex balance of costs and benefits occurring simultaneously at multiple spatial scales.

Although a key objective of our study design was to evaluate differences in roost selection by multiple species in the same landscapes, our data indicate considerable similarity among the snags selected by the 3 species. Previous studies have reported differential use of tree species among sympatric bats (Boonman 2000, Chung MacCoubrey 2003), but tree species was not an important factor

differentiating use by bats in our study area. Moreover, there was considerable overlap in structural and contextual characteristics of snags and trees used as roosts by the species we studied. The only pronounced differences in use of roosts and roosting behavior were greater variability in types of roosts used by long-eared myotis (which used conifer and hardwood trees and snags, rocks, logs, and stumps) and tendency for long-eared myotis to roost close to capture sites (e.g., water or bridges). Although mean diameter of snags used by long-eared myotis was smaller than for the other species, long-eared myotis roosted in a variety of snags, a number of which had characteristics similar to those of the other species. Moreover, although big brown bats and long-legged myotis did not use rock crevices in our study, they use them in other regions (Cryan et al. 2001, Lausen and Barclay 2002, Baker and Lacki 2006). The high degree of overlap in selection of snags among species suggests that other aspects of the natural history of these species, such as foraging ecology, may be critical for niche separation. Alternatively, it is possible that some partitioning of the roost resources occurs based on either characteristics or at a spatial scale (e.g., micro-selection within a snag) that we did not measure. It is also possible that some subtle temporal partitioning of the roost resources exists. However, we have no direct evidence that any of this occurs. Our observations and published data for different species using the same roosts simultaneously or over short time periods suggest that partitioning of roost resources is unlikely.

Understanding topographic context associated with roosts is likely important for a complete understanding of the roosting ecology of bats in temperate forests. Although many of the relationships between elevation and roost

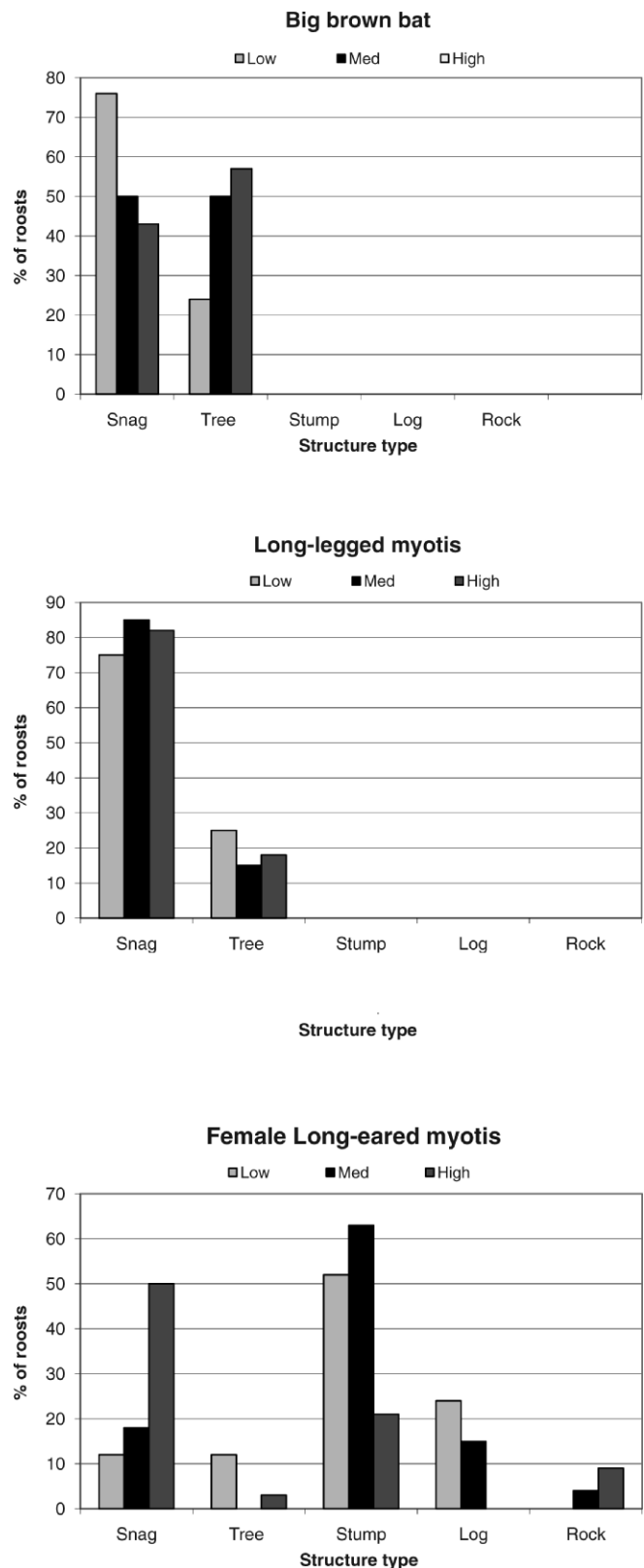


selection are manifested at broad spatial scales that were not our focus, big brown bats roosted in snags that were lower in elevation than randomly selected snags. Elevation was a variable in a competing model describing selection of roosts by long-legged myotis from random trees. We surmise that females in our study may choose areas to roost based in part on compromises between densities of snags suitable for roosting and elevation (Arnett 2007) and perhaps on other factors. At broad spatial scales, female bats generally occur less frequently at higher elevation sites (e.g., Grindal et al. 1999, Cryan et al. 2000, Baker and Lacki 2006, Arnett 2007). Female bats likely benefit from roosting at lower elevations because of warmer temperatures or higher prey abundance (Grindal et al. 1999, Cryan et al. 2000, Kunz and Lumsden 2003). Broders et al. (2006) hypothesized that if bats use several roosts with different exposures and insulating properties, individuals could select roosts on particular days that optimize thermal benefits depending on ambient conditions. Although we found that bats used roosts on several different aspects, we have no direct evidence of obvious patterns of use of different aspects in relation to nightly temperature or other factors.

The 3 species of bats we studied rarely used snags in young forests, especially in clear-cuts, even when potential roosts were available, which is consistent with findings that bats typically roost in older forest stands (e.g., Campbell et al. 1996, Crampton and Barclay 1998, Cryan et al. 2000, Kunz and Lumsden 2003). Although bats often roost in sites with less canopy closure, snags that are taller than surrounding canopy, or those occurring on an edge (Hayes 2003, Barclay and Kurta 2007), there may be a threshold beyond which increased solar radiation is not beneficial to bats. Alternatively, bats may avoid roosts in clear-cuts and young forests because of increased risk of predation. Snags typically occur in lower density in clear-cut harvest units (Ohmann et al. 1994, Arnett 2007) and often are individual, prominent structures that may attract predators differentially than do snags located on edges or within forests. This hypothesis, although plausible, currently is not supported with empirical evidence.

We found that long-eared myotis used a variety of structures as roosts, similar to other studies (Vonhof and Barclay 1997, Rabe et al. 1998, Waldien et al. 2000, Rancourt et al. 2005), but relative use of different types of structures varied with landscape. Long-eared myotis used stumps and down logs most extensively in landscapes with low densities of snags, and used snags as day roosts more often in landscapes with high snag densities, corroborating Waldien et al. (2000). By using a wide variety of types of structures for day roosts in forested landscapes, long-eared myotis may be able to adjust to differing availability of different types of structures in the landscape (Waldien et al. 2000), thus taking advantage of otherwise inhospitable habitat and possibly avoiding competitive interactions with sympatric species when snags are limited.

We assume our analyses are representative of females of the 3 species of bats we studied. There are important



**Figure 4.** Percentage of different types of structures used as day roosts by female big brown bats, long-legged myotis, and long-eared myotis in landscapes with estimated low (<2.7 snags/ha), medium (2.7–5.5 snags/ha), and high (>5.5 snags/ha) densities of snags the western Oregon Cascades, 1999–2001.

differences between reproductive and nonreproductive females, as well as variability between years, however, which could have been masked by pooling data (Miller et al. 2003, Barclay and Kurta 2007). By sampling multiple, randomly selected landscapes distributed throughout the western Oregon Cascades, our findings likely reflect patterns of roost use in coniferous forests in this region, but variation among landscapes and small sample sizes limits our inferences.

## MANAGEMENT IMPLICATIONS

In Douglas-fir forests west of the Cascade Range, retaining large (>50.8 cm dbh) snags that protrude above the canopy, reside near a gap or stand edge, or have less canopy closure, in a variety of topographic settings, will provide roost habitat for multiple species of bats. Although large, solitary snags can provide roosts for species such as big brown bats, retaining patches of snags will likely increase probability of use for the species we studied. Although snags within riparian areas benefit numerous species of wildlife (e.g., Hagar 1999), they are not extensively used by bats (e.g., Campbell et al. 1996, Ormsbee and McComb 1998, Waldien et al. 2000, this study) and managers should provide snags in upland habitats. We also found that bats rarely roosted in snags in stands <40 years old; providing snags in forest age classes >40 years old will increase the probability of use by bats in this region. Some species of bats alter selection of roosts depending on landscape context and availability of different types of roosts, and forest managers must consider the needs of multiple bat species and the distribution of roosts in the landscape. Managed landscapes, especially those at lower elevations, can provide suitable habitat for female bats but not in the absence of numerous snags and replacement green trees in locations where they are most likely to be used.

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**Appendix.** Candidate model set ( $n = 27$ ) for differentiating between roost and random snags for female big brown bats, long-legged myotis, and long-eared myotis in forests in the western Oregon Cascades, 1999–2001.

No.	Model statement
1	Null
2	Dbh
3	Ht
4	Bark
5	No. of small snags
6	No. of large snags
7	% canopy
8	Aspect
9	Elevation
10	Distance to edge
11	Solar
12	Distance to capture site
13	Distance to stream
14	Dbh + no. of small snags
15	Dbh + no. of large snags
16	Dbh + aspect
17	Dbh + distance to edge
18	Dbh + elevation
19	Dbh + distance to capture site
20	Dbh + distance to stream
21	Dbh + no. of smalls snags + interaction
22	Dbh + no. of large snags + interaction
23	Dbh + aspect + interaction
24	Dbh + distance to edge + interaction
25	Dbh + elevation + interaction
26	Dbh + distance to capture site + interaction
27	Dbh + distance to stream + interaction